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AN UNUSUAL OCCURRENCE OF ORNITHODOROS MOUBATA (ARACHNIDA)

By T. W. CHORLEY, F.R.E.S.1

Ornithodoros moubata Murray, like other Argasidae, is seldom found on its host, since it normally feeds only at night and hides in cracks or among dust during the day; I do not know of any record of the species being found in

numbers on a host away from the dwelling of the latter.

During a recent tsetse-survey in Karamoja, the easternmost district of Uganda, I shot two wart-hogs (*Phacochoerus aethiopicus* ssp.), of which one bore 42 specimens of *O. moubata*, in addition to a few Ixodid ticks, while the other was infested with Ixodids only. The ticks were not attached to the skin but were crawling about freely. They were mainly on the nape of the neck

and along the ridge of the back.

It seems likely that the wart-hog infested with *Ornithodoros*, which was shot at about 10.0 a.m., had just left its burrow, though there is no evidence of this, and a circle of about 200 yards radius from the animal was searched without a burrow being found. Wart-hogs were very plentiful in the area. The locality was about ten miles from the nearest permanent human habitations, but there are temporary camps in the area every year for the grazing of sheep and goats. *Ornithodoros moubata* is not known to infest huts in Karamoja, but this means little, because Karamoja is the least known district in Uganda.

The new record bears some resemblance to that of Lloyd (1919: 559), who captured about thirty specimens of *Ornithodoros* on an African who had been searching for tsetse-pupae in a wart-hog burrow in Northern Rhodesia. The most striking differences between the two records are that the ticks found by me were not feeding and that the host was evidently at some distance from its burrow. As in Lloyd's case, no very large specimens were among the ticks

collected.

REFERENCE.

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¹ Published by permission of the Director of Medical Services, Uganda.

THE OCCURRENCE OF THE TICK PARASITE IXODIPHAGUS CAUCURTEI DU BUYSSON (HYMENOPTERA; CHALCIDOIDEA; FAM. ENCYRTIDAE) IN GREAT BRITAIN

By E. T. BURTT.

(Entomology Department, London School of Hygiene and Tropical Medicine.)

In the course of work on the sheep tick (Ixodes ricinus L.) under the auspices of the Agricultural Research Council, I visited Cumberland in September, 1942, to collect gorged nymphs to supplement our laboratory culture. I collected 587 gorged nymphs of I. ricinus from sheep at Crag Farm, Eskdale, between September 29th and October 1st. These were brought back to London and subsequent incubation resulted in hymenopterous parasites emerging from two of the nymphs: $2 \circlearrowleft$ and $3 \circlearrowleft$ from one on November 9th, and $2 \circlearrowleft$ and $4 \circlearrowleft$ from the other on November 28th, making a total of 11 specimens.

Mr. G. E. J. Nixon of the Imperial Institute of Entomology kindly identified them for me as Ixodiphagus caucurtei du Buysson. According to Gahan (1934), Ixodiphagus caucurtei du Buysson is the same insect as the tick parasite Hunterellus hookeri Howard, which means that the earlier records variously

given under both these names only refer to one insect.

I have been unable to find any previous record of I. caucurtei in Great Britain. Macleod (1932) states that he did not find it in over 1000 gorged nymphs of Ixodes ricinus collected from sheep in the Ettrick Valley in the spring of 1931. The geographically nearest records are from northern France. Du Buysson (1912), in his paper describing Ixodiphagus caucurtei, mentions that the Chalcids were obtained by Dr. Brumpt from nymphs of Ixodes ricinus L. found on deer at Chantilly in October, and Fontainebleau in November. Brumpt (1913) found the insect from April to November in France and in two lots of nymphs of Ixodes ricinus collected from deer found 10 out of a hundred

parasitised in one case and 17 out of a hundred in the other.

Gahan (1934) summarises the records of Ixodiphagus caucurtei and Hunterellus hookeri up to that date, and it is obvious that the parasite is widely distributed over the world, and that it attacks species from most of the genera of Ixodid ticks. Thus in Africa it has been found in Durban attacking Haemaphysalis leachi Audouin, at Pretoria on Hyalomma aegyptium impressum Koch, at Lourenço Marques on Rhipicephalus evertsi Neumann. On the western side of the continent it has been recorded from Rhipicephalus sanguineus Lat. at Lagos and from Rhipicephalus at Conakry in French Guinea. Its range eastwards is indicated by records from Indo-China and Southern India. ing to the New World; there is a record from an unidentified tick at Rio de Janeiro in South America; another from Dermacentor nitens Neumann in Porto Rico and a third (again from an unidentified tick) from Havana, Cuba. The distribution in North America is complicated by the fact that the parasite has twice been introduced from France in attempts to control ticks of the genus Dermacentor: once in 1927 at Naushon Island, Mass., against Dermacentor variabilis Say: and again, in 1928, on a much larger scale in Montana as part

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of the control measures against D. andersoni Stiles, the vector of Rocky Mountain Spotted Fever. It is also endemic and has been found in Mexico on Rhipicephalus sanguineus, in Texas on Rhipicephalus texanus Banks, in California on Dermacentor parumapertus Banks (= variabilis Say), in Florida on Rhipicephalus sanguineus, and in South Carolina on Dermacentor variabilis Say.

Ixodiphagus caucurtei is not exactly a conspicuous insect and doubtless it still remains to be found in many new localities; for example, it has not yet been reported from Australia. Cooley (1929) considers that it is probably a species of tropical origin because he got very heavy mortality when he tried to delay its development during the winter by subjecting it to low temperatures,

and finally decided that it did best if bred continuously.

Cooley (1929) summarises what is known of the life-history and habits, and Morton (1929) describes a method by which the tick parasites may be reared in large quantities. Wood (1911) describes Hunterellus hookeri seeking out the nymphal ticks on the mammal host (apparently a rabbit in his case) and "crawling through the hair as naturally as a flea." Parasitised ticks have been found on rabbits, dogs, deer, and on sheep in my own record; so it appears that the Chalcid is as impartial to the mammal host on which the ticks are attached as it is to the genus of ticks which it parasitises.

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A NOTE ON ORTHOPELMA LUTEOLATOR GRAV. AND O. BREVI-CORNIS MORL. (HYMENOPTERA, ICHNEUMONIDAE)

By E. McC. Callan, B.Sc., A.R.C.S., D.I.C., Ph.D., F.R.E.S.

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Introduction.

A STUDY of the community of insects inhabiting the galls of three species of the Cynipid genus *Rhodites* in England afforded an opportunity of comparing the Ichneumonid parasites *Orthopelma luteolator* Grav. and *O. brevicornis* Morl.

The larvae of *Rhodites* cause galls of distinct and characteristic appearance on various wild roses. R. rosae (L.) is the most abundant species and produces the gall known as the robin's pincushion, moss gall or bedeguar. R. eglanteriae Htg. gives rise to the smooth pea gall, and R. rosarum Gir. to the spiny pea gall.

Galls were collected in 1934–36, the majority being obtained from 26 localities in south Buckinghamshire within 20 miles of Slough, but some were collected from a number of localities in Hampshire, Surrey, Cumberland and Yorkshire.

The galls were kept in glass tubes and jars capped with muslin until the insects appeared. These were stored in an improvised outdoor insectary in which conditions of temperature and humidity approximated those in the open air.

Previous Records.

O. luteolator is a well-known parasite in Europe of R. rosae. It has been recorded as such by Brischke (1882), Morley (1907), Ruschka and Fulmek (1915), Hoffmeyer (1925), Picard (1926), Voukassovitch (1928) and Poulton (1937) among others. It has also been recorded as a parasite of R. eglanteriae by Brischke (1882) and Morley (1907).

O. brevicornis was described by Morley (1907), who stated that he had seen only two individuals, which were both females and without host records. It appears to be a rare insect in England and nothing has hitherto been published

on its host relations.

Specimens Reared in England.

O. luteolator was reared from both R. rosae and R. eglanteriae. Specimens from R. eglanteriae were distinctly smaller than those from R. rosae, and males and females were obtained in about equal proportions. The parasite was obtained in great abundance from R. rosae from every locality where galls were collected. In all 513 out of 815 bedeguar galls of R. rosae produced 5706 specimens of O. luteolator; 1894 of these were males and 3812 females, the sex ratio being approximately 1 male: 2 females.

O. luteolator appears only to parasitise R. rosae and does not attack any of

the other species of insects inhabiting the galls.

A number of galls were isolated in 1935 from the main bulk of the collected material, and observed, usually daily, for the appearance of insects over a period of 14 weeks. The time and the length of the period of appearance of O. luteo-PROC. R. ENT. SOC. LOND. (A) 18. PTS. 4-6. (JUNE 1943.)

lator and that of its host were closely parallel. Males and females of O. luteolator appeared from 13 May to 5 July, and from 22 May to 14 July respectively. Females of R. rosae, which is a parthenogenetic species, started to appear on 14 May and continued until 17 July. There was a very clearly defined peak of appearance for both the parasite and its host on 1 July.

 \hat{O} . brevicornis was reared from both R. eglanteriae and R. rosarum. Only ten individuals were obtained altogether, four females from R. eglanteriae and

four females and two males from R. rosarum.

A number of specimens of both O. luteolator and O. brevicornis have been placed in the collection at the British Museum (Natural History).

Comparison of Orthopelma luteolator and O. brevicornis.

Various comparative measurements of the two Orthopelma species were made. The degree of variation occurring in O. luteolator was first determined from random samples of 100 males and 100 females. In the determination of the variation in the number of antennal segments in this species, the antenna was taken to include the scape, pedicel and flagellar segments. Occasionally the antennae were heteromerous, due to the fusion of the terminal and penultimate segments of one antenna, and the antennal number was then expressed in the form 19, 20 instead of 19 or 20.

Table 1 shows the antennal variation in O. luteolator, 94 per cent. of the males having 21 to 22 and 90 per cent. of the females 18 to 19 antennal segments.

TABLE 1.

Number of	Orthopelma luteolator		Orthopelma luteolator	
antennal segments	Percentage of males	Percentage of females		
17 18 19 19, 20 20 21 21, 22 22 22, 23 23	- - 3 31 4 59 2	5 11 79 3 2 — —		

The ovipositor palps and nervus parallelus of the wing were measured in the females of both species. In O. luteolator the range of variation in the length of the ovipositor palps was 0.65-1.13 mm., with a mean value of 0.95 mm, and in the nervus parallelus of the wing 0.52-0.80 mm., with a mean value of 0.72 mm. The nervus parallelus was measured in preference to a more direct measurement and was taken as being proportional to the size of the insect. The quantity—Length of ovipositor palps/Length of nervus parallelus (L.op/L.np)—is independent of size and was used for comparison of the relative lengths of the ovipositor palps in the two species.

The area superomedia of the thorax, which lies dorsally and posterior to the postscutellum, was also measured and compared in the two species. In

O. luteolator it is short and broad and in O. brevicornis long and narrow.

Table 2 shows the females of O. luteolator and O. brevicornis compared.

TABLE 2.

	Orthopelma luteolator from R. rosae	Orthopelma brevicornis	
		from R.	from R . eglanteriae
Number of specimens	100 19 0·95 0·72 1·3 0·25 0·20	4 16 0·41 0·78 0·5 0·35 0·15	4 16 0·36 0·74 0·5 0·35 0·15

Key for the Separation of Orthopelma luteolator and O. brevicornis.

Females of O. luteolator and O. brevicornis can be separated by the following

- 1. Antenna of female 19-segmented; length of ovipositor palps of female 0.95 mm., L.op/L.np 1.3 mm.; area superomedia a little longer than broad $(0.25 \times 0.20 \text{ mm.})$. . luteolator Grav.
- 2. Antenna of female 16-segmented; length of ovipositor palps of female 0.38 mm., L.op/L.np 0.5 mm.; area superomedia a little more than twice as long as broad $(0.35 \times 0.15 \text{ mm.})$ brevicornis Morl.

ACKNOWLEDGEMENTS.

The work was carried out at the Imperial College of Science and Technology Biological Field Station, Slough, Bucks, in the course of an investigation of the community of insects inhabiting the galls of three species of *Rhodites*.

I wish to express my deep indebtedness to Professor J. W. Munro and Dr. O. W. Richards, under whose supervision the work was carried out, for their interest, advice and constructive criticism during the progress of the investigation.

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NATURAL RESERVOIRS OF SOME BEETLES OF THE FAMILY DERMESTIDAE KNOWN TO INFEST STORED PRODUCTS, WITH NOTES ON THOSE FOUND IN SPIDER WEBS

By H. E. HINTON, Ph.D.

Department of Entomology, British Museum (Natural History).

This paper contains a brief summary of the Dermestidae known to occur in the nests of bees and wasps, gregarious caterpillars, birds, and rodents, and a more detailed account of the habits of a few species which live on the accumulations of dead insects found near the webs of some spiders.

I have to thank Mr. E. Browning for his help in determining the spiders, and Mr. G. V. Carvell, Dr. A. S. Corbet, and Dr. O. W. Richards for their

collections of cobwebs.

DERMESTIDAE in bee and wasp nests.

It has long been known that the nests of bees and wasps serve as reservoirs and even original sources of a number of stored product pests. From an economic point of view these nests may occasionally deserve attention in so far as they serve to maintain small and widely distributed populations which may at any time serve as foci for infestations of stored products. Our knowledge of the occurrence of stored product pests in the nests of Aculeate Hymenoptera has recently been summarised in an interesting paper by Linsley (1942). Ptinus fur L., for instance, has been found in the nests of both solitary and social bees and wasps. The confused flour beetle, Tribolium confusum J. du V., occurs in the cells of the bees Anthophora, Osmia, and Clisodon in California. In Britain 16 species of Cryptophagus are found in granaries and warehouses, and of these no fewer than nine also occur in the nests of bees and wasps where they feed on moulds.

Among the Dermestidae are to be found many species, including some of considerable economic importance, which are able to maintain themselves in bee and wasp nests, e.g. Dermestes lardarius L., D. murinus L., Attagenus pellio L., A. piceus Oliv., A. pantherinus Ahren, Megatoma undata L., M. vespulae Milliron, Globicornis corticalis Eichh., Anthrenus fuscus Oliv., A. scrophulariae L., A. verbasci L., A. museorum L., Trogoderma ornata Say, T. versicolor Creutz., T. glabrum Herbst, and T. ajax Casey. These Dermestids live mainly on dead bees and wasps. The adults, except of the genus Dermestes, if they feed in the nests, probably feed only on pollen and honey. The adults of D. lardarius have been recorded feeding on wax and pollen in bee hives, and their larvae are said to attack the bee larvae. Some species indirectly kill the bees by opening the cells and exposing the immature stages to the external environment, e.g. Anthrenus scrophulariae is recorded killing the young of Osmia in this way.

It is evident that quite a high percentage of the insects that attack stored products are able successfully to colonise bee and wasp nests, and a few, e.g. the lesser wax moth, *Achroia grisella* F., are primarily bees' nest insects. In practice the nests of Aculeate Hymenoptera are rarely of even slight importance as reservoirs of injurious Dermestidae, and in this respect cannot be

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compared with either bird (chiefly sparrow) or spider nests which, because of their greater abundance and proximity to houses and warehouses where stored products are kept, are a factor to be reckoned with in the control of these beetles.

DERMESTIDAE in nests of caterpillars.

In Europe a few Dermestidae are known to breed in the nests of certain gregarious caterpillars of the families Thaumetopoeidae and Lymantridae. Dermestes mustelinus Er., D. aurichalceus Kuster, D. lardarius L., and Anthrenus vorax Waterh. are found in the nests of Thaumetopoea pityocampa Schiff. Dermestes aurichalceus has also been recorded in the nests of T. processionea L. D. erichsoni Ganglb., and D. tessellatus F., have been found in the nests of the brown-tail moth, Euproctis chrysorrhoea L., and the former also in the nests of Euproctis similis Fuess. The larvae and adults of the species of Dermestes feed on the dead or injured moth larvae. Dermestes mustelinus is said to be of some value in controlling T. pityocampa in Catalonia.

DERMESTIDAE in bird and rodent nests.

Bird nests also serve as reservoirs of injurious Dermestiale, e.g. Dermestes lardarius L., D. bicolor F., D. nidum Arrow, Attagenus piceus Oliv., A. pellio L., Anthrenus fuscus Oliv., A. verbasci L., A. scrophulariae L., and A. pimpinellae F. In Germany sparrow nests are the chief source of household infestations of Attagenus piceus, A. pellio, Anthrenus verbasci, and A. scrophulariae. The larvae of all these species as well as the adults of the genus Dermestes feed on the remains of insects, feathers, dead birds, etc. Dermestes larvae probably also attack and even occasionally kill the young birds. The larvae of both D. bicolor and D. lardarius are not uncommon in pigeon lofts in Germany, where they have been recorded injuring, and even killing, the young pigeons by boring into their wings. Both species have also been known to attack and kill newly hatched ducklings and chickens, particularly where there are pigeon lofts, from which the infestations usually originate, above the poultry houses. Rodent nests may be found on investigation to be capable of supporting small populations of Dermesteridae; e.g. Attagenus piceus Oliv. has recently been recorded breeding in chipmunk nests in California.

DERMESTIDAE in spider nests.

A source of dead insects which is utilised by some beetles is provided by species of tube and sheet web-building spiders which accumulate dead insects, often in considerable numbers, near their webs. These collections of insect remains have scarcely been investigated. The only beetles ¹ that appear to have been successful in invading this type of habitat are, as might be expected, the larvae of a few Dermestidae.

Seven species of Dermestidae have been recorded in or near spider webs, Attagenus pellio L., Ctesias serra Steph., Megatoma undata L., Globicornis marginata Payk., Trogoderma ornata Say, Anthrenus museorum L., and Trinodes hirtus F. A further species, Anthrenus fuscus Oliv., has recently (vi.—xi.1942) been found by me to be very common in Linton and Little Abington, Cambs., about stone walls, sheds, barns, and houses in or about the webs of Tegenaria

¹ A Lathridiid, *Melanopthalma* sp., is found in large numbers in the nests of a Mexican social spider, *Coenothele gregalis* (Diguet in Wheeler, 1928, *The social insects*). This beetle is a commensal and probably, like many of its congeners, feeds only on fungi.

domestica L., and other spiders. A. museorum frequently occurred in the same webs. The larvae of both species of Anthrenus are also very common in spider webs about sheds and outhouses in Reading (A. S. Corbet) and Slough (O. W. Richards). A few larvae of both species were found by me during the summer of 1942 under bark in Linton with the spiders Cinifio ferox Walck., Clubionia corticalis Walck., Harpactea hombergii Scopoli, and Segestria senoculata L. The breeding habits, out of doors, in Britain of these two species

of Anthrenus do not appear to have been previously known.

As regards their host relationships, the Dermestid larvae may be described as scavengers and facultative predators. All appear to live mainly on dead insects, spiders, and wood lice, but it seems probable that most species will occasionally feed on eggs and young spiders within the egg sacs. Auten (1925) has shown that in Ohio the larvae of Trogoderma ornata are common under bark in the nests of Aranea frondosa and Epeira sclopotaria where they frequently bore into the egg sacs in order to eat the eggs or freshly hatched spiders. Both Anthrenus museorum and A. fuscus are often found in egg sacs near webs, but they do not appear to enter undamaged egg sacs. They will, however, bore into egg sacs that contain dead eggs or dead young. It sometimes happens that, for one reason or another, a few eggs or freshly hatched young have died, or the egg sac has been injured, and the Anthrenus larvae having entered the egg sac for these will, after consuming them, no doubt attack the uninjured eggs and young. D. lardarius larvae, for instance, readily bore into injured silkworm cocoons, but are unable to penetrate sound cocoons, and will only exceptionally gnaw the latter.

It is evident that Dermestid larvae living in such close proximity to spiders must in some way be protected from the attacks of these notably aggressive arachnids. Keeping in mind the fact that each larva probably lives from about seven months to three years or so, more or less exposed to the attention of the spiders, it becomes abundantly clear that if an individual is to survive it must be relatively immune from attack. How, then, is this immunity achieved? This question may be fully answered by considering each case concretely, for the different species appear to be protected in different ways, as is shown below under the headings of the various species. All species are, however, alike in two respects. Firstly, they are all densely clothed with long and stiff bristles, for which reason alone they are probably unacceptable to most spiders. Bristowe (1941) has shown that caterpillars clothed with stiff bristles are invariably rejected by hunting spiders, e.g. Clubionia, Scotophoeus, Harpactea, etc., and frequently rejected by Argyopids and others. Secondly, they are all able to crawl quickly, and without being entangled, on the sheet webs of Tegenaria, and over the day cells of Clubionia, Harpactea, etc. Both Anthrenus and Ctesias were placed on several occasions in the orb webs of species of Aranea but were unable to make any progress due to the stickiness and distance apart of the strands. Needless to add, they are never found. under natural conditions in orb webs.

Ctesias serra F.

The larva of this European species is very common under loose bark in Britain, where it is nearly always found in or about spider webs, feeding on the remains of insects killed by the spiders. A summary of the literature relating to this species has been given by Donisthorpe (1920). Waterhouse (1834) first drew attention to its association with spiders, pointing out that it was invariably found in company with a particular species of spider that spins a web-like case. Waterhouse believed that the larvae fed on the spiders. Other writers have also noted the fact that it is found under bark in cobwebs (Westwood, 1839; Sharp, 1899; Dollman, 1913; Joy, 1920), but in no case are the names of the spiders given. Many writers have found the larvae feeding on the remains of dead insects under bark but have either not found them in or near spider webs, or else have failed to notice their partial dependence on the stores of dead insects accumulated by the spiders. Grenier found the larvae feeding on the eggs of the gypsy moth, and in this connection it is interesting to note that this habit has been recorded for other DERMESTIDAE.²

The larvae have also been reported feeding on paper, dry bread crusts, and on cobwebs. I have often found that larvae kept in captivity would eat through paper and through webs, and I once found several larvae which had eaten holes through a moth cocoon in order to get at the pupa. The considerable damage often done by the mature larvae of such species as *Dermestes maculatus* Deg., *D. frischi* Kug., and *D. lardarius* L., to cotton, linen, tobacco, wood, cork, and even metals when seeking a suitable site in which to pupate is already well known. Larvae of *C. serra* confined with paper and cobwebs

alone starved.

The adult lays about 40 eggs under bark, and these hatch in 15–21 days. The larvae usually moult five or more times. They pupate in the spring, and the last larval skin remains attached and almost entirely enclosing the pupa. Joy (1920) claims in error that the larvae construct a "webbed-cocoon" in which to pupate. The pupal stage lasts about two weeks, and the adult remains within the last larval skin for a few days before emerging. The

winter is apparently always passed in the larval stage.

During the period May-November 1942 many larvae were found in Linton and Little Abington, Cambs., beneath loose bark of dead or live pine, fir, elm, willow, and oak trees. The larvae were always found in or near the webs of Segestria senoculata L., Harpactea hombergii Scopoli, Clubionia corticalis Walck., or Ciniflio ferox Walck. On one occasion a specimen of Scotophoeus blackwalli Thor., was taken with the larvae. Altogether more than 200 larvae were collected, many of them actually crawling over the cells of Clubionia and Harpactea. In a few instances they were found feeding on dead specimens of Forficula auriculata L. This earwig was often abundant under bark, and occasional dead specimens could be found not far removed from spider webs. The spiders may have been responsible for killing the earwigs. Bristowe (1941) found that in captivity Segestria senoculata would accept earwigs. one occasion several larvae were found that had bored through a moth cocoon and were feeding on the pupa. I have also seen three larvae, which were collected in a Cossus burrow, feeding on the dead caterpillar (Kew Gardens, ix.1942, Fraser-Brunner).

C. serra was most frequently found in company with Clubionia and Harpactea, but Cinifio and Segestria were not uncommon, and occasionally all four would be found under bark within an area of a few square inches. As

² In Morocco de Lépiney found that the egg masses of the gypsy moth are destroyed by Anthrenus verbasci L., and Trogoderma versicolor Creutz., the latter species playing in this way an important part in controlling the gypsy moth on cork oak. In the U.S.S.R. Dermestes erichsoni Ganglb., and a species of Attagenus have also been found feeding on the egg masses of the gypsy moth. In the United States the larvae of Anthrenus verbasci L., and Megatoma variegata Horn, have been found destroying the egg masses of tussock moths. The activities of Dermestes lardarius L., and D. coarctatus Har., as predators of silkworm eggs are well known. Some of the species of Thaumaglossa appear to be obligatory predators of Mantid eggs.

has already been noted, the larvae were usually near the spiders and sometimes were only separated from them by the thickness of a web. No evidence of any kind, e.g. "chewed" larvae, was found to suggest that the spiders ever attack the larvae. A Clubionia (sp.?) and Harpactea hombergii were confined without food but with numerous larvae for over two months, and during this time, as far as could be discovered, no attempt was made to attack the larvae. The larvae are a suitable size for attack, i.e. they are appreciably smaller than the spiders and yet are, except when very young, more than one-sixth as long as the bodies of most of the spiders with which they were found. Their immunity from attack may be due to their taste, but this seems unlikely in view of the fact that Tegenaria domestica did not hesitate to eat them. It is, however, not impossible that they are distasteful to the spiders with which they are found, as different spiders are known to have different tastes. In short, their immunity from attack appears to be due primarily to two factors: (1) they are densely clothed with long, stiff, densely spinose bristles and numerous, easily detached, spear-headed hairs; and (2) they have developed certain characteristic warning movements which they readily use when threatened.

There are two kinds of warning movements. Firstly, the erection of the dorsal abdominal tufts of spear-headed hairs, and, secondly, the rapid vibration of the caudal brush of long and slender hairs. The sides of the posterior region of four abdominal tergites (fourth to seventh inclusive) are membranous and nearly vertical, and from these membranous areas arise dense tufts of multi-segmented, spear-headed hairs. These tufts are normally sub-recumbent, but when the larva is touched or alarmed in some other way, they are rapidly erected and expanded, so that the larva immediately looks about half again its normal size. At the same time as these tufts are erected the larva often turns rapidly around in order to present the tufts to the point of attack. The spear-headed hairs of which the tufts are comprised are very readily detached, and it is possible that they easily penetrate the cuticle of the spider and set up an irritation of, at any rate, a mechanical type. As the tufts are erected the brush of long and slender hairs on the apex of the eighth abdominal segment is often vibrated very rapidly, the apices of the hairs describing an arc of 10 to 40 degrees. According to Donisthorpe (1920), a larva survived for a fortnight in an ants' nest, during which time it was mainly protected from the attacks of the ants by the vibrations of the caudal brush. Bristowe (1941) has shown that the rapid vibration of antennae, wings, legs, etc., is not infrequently used by insects in order to secure immunity from the attacks of spiders. Seven larvae were placed at various times in four webs of Tegenaria domestica, and all were eaten in spite of the fact that they were plainly seen to erect their dorsal tufts and vibrate their caudal brush. These spiders usually struck at the hind end of the body. On one occasion a Tegenaria bit the tufts above the body, pulled out most of the spear-headed hairs, and then returned, after wiping its mouth, to a successful attack. On a few occasions willow trees harbouring many larvae have been found within a few yards of outhouses, but in no instance have the larvae of C. serra been found in outhouses or houses. These facts suggest that Tegenaria and other semi-domestic spiders prevent the establishment of C. serra in sheds, barns, and houses.

Megatoma undata L.

This species is widely distributed in Europe and Asia. It has been found on skins and furs, and there are a number of records of its occurrence in houses

in Britain, France, and Germany. The only record of its occurrence in spider webs is that of Morison (1931), who found the larvae feeding on moth pupae

and other insects entangled in webs on a fence in London.

The adults appear to be pollen feeders, and in the spring and early summer occur on flowers, e.g. hawthorn and crab-apple. The larvae normally live as scavengers under bark, or in the nests of bees and wasps, or in the burrows of Coleoptera and Lepidoptera, where they feed on the remains of insects. The larvae have been found in Poland feeding on the hibernating larvae of Pseudoclavellaria amerinae L. It is probable that it is rarely a predator on larvae or adults, but it may more often attack eggs and pupae, particularly if the latter are injured.

Attagenus pellio L.

This cosmopolitan species is well known for the damage it causes to many kinds of animal products. The larva is sometimes a serious pest of furs, skins, woollens, carpets, upholstered furniture, smoked meat and fish, casein, etc., and has also been recorded attacking dried museum specimens, particularly insects. It has been found destroying silkworm cocoons and pupae, bolting silk used in flour mills, and will feed on artificial silk that has been heavily dressed with starch. Larvae have been found in flour, meal, rye bran, and other farinaceous materials, but in these instances it may have been feeding on the remains of other insects. It is not yet certain that it can develop on a diet consisting only of materials of vegetable origin.

It is often found in bird nests, hen-coops, and pigeon-cotes. Hayhurst (1940) has often found the larvae in Britain in insect remains accumulated from spider webs. Several larvae were found by me associated with spiders in houses at Linton, Cambs., during 1942: 24.v., one larva in the remains of insects accumulated beneath the web of *Tegenaria domestica* L.; 7.vi., many cast skins among insect remains and spider webs (sp.?) under loose wall paper;

and 29.ix., one larva in a spider's web (sp.?) under loose wall paper.

Very little is known of the life-history of this species. The adults are found in the spring and early summer on the flowers of wild plum, hawthorn, *Spiraea*, and other plants. They feed only on pollen and nectar. Up to 50 eggs are laid by each female. In Britain the larvae which hatch in the early summer do not pupate until the following spring, but Zacher found that in Germany the larvae usually pupate in the autumn, and the winter is passed in the adult stage. According to this writer, there is usually one generation a year in Germany, but a generation may take as much as three years.

Trogoderma ornata Say.

The larva of this North American species has been recorded attacking dried insects, stuffed birds, and other museum specimens as well as skins, furs, woollens, and feathers. It has been found feeding on maize meal, sweet corn, popcorn, and nuts, and it will develop on the seeds of Ambrosia trifida and Euthemia graminifolia. Very little is known of the habits of this species out of doors. In Ohio Auten (1925) has found the larva under bark in the nests of two species of spiders, Aranea frondosa and Epeira sclopotaria. The larvae were feeding on the eggs of these spiders, and, in the late summer and early winter, were responsible for destroying many nests, and would even eat into egg capsules containing young spiders.

Globicornia marginata Payk.

This species is confined to Europe, where its larvae have been found on a number of occasions under bark or in holes in trees, feeding on dead insects. It has twice been recorded under bark in cobwebs (Rosenhauer, 1882; Formanek, 1900).

Anthrenus fuscus Oliv.

This species occurs in Europe, Japan, Assam, and North America. There are a few records of its occurrence in houses and warehouses in Britain and on the Continent. It has not previously been recorded damaging commodities, but a few larvae have recently been found in stored blankets in Surrey (E. B. Cooke). I have found that the larvae will apparently develop normally when fed on wool alone. According to Kunike, larvae offered a choice of wool and dead insects preferred the latter. Anthrenus fuscus is not uncommon in entomological collections in Britain, though I am unable to find any records of its occurrence in these situations. I have found it attacking insect collections in the University Museum of Zoology, Cambridge, and in the British Museum (Nat. Hist.).

Very little is known of the life-history of this species. In Linton, Cambs., the adults are found on flowers from the beginning of May to the middle of August. The adults feed, like all other species of Anthrenus, on pollen and nectar, and will not eat dead insects. In Linton they have been found on the flowers of parsley, cow parsley, privet, American Pillar rose, and two species of daisy, and of these they showed a marked preference for those of parsley. The adults frequently copulate on the flowers during the day. In the laboratory the females oviposited readily on dead beetles of various kinds, Tipulids, moths, and bees. The eggs were usually well concealed in the pubescence of the dead insects. At 30° C. \pm 1° the eggs hatch in 10–11 days, but this temperature is almost certainly above the optimum. Out of doors larvae which hatch in the spring or early summer do not pupate until April or May of the following year. A larva kept at 30° C. \pm 1°, and fed on the abdomen of a moth, had moulted seven times 112 days after hatching. At 25° C. ± 1° the pupal stage takes 5-6 days, and after emerging from the pupa the adults remain quiescent within the last larval skin for 4-5 days. As is usual in the Dermestidae, the pupa is almost entirely enclosed by the last larval skin. Pupation occurs among the remains of insects below the webs or in disused webs, but pupae of this species and A. museorum have been found on a few occasions attached to the lower surface of occupied sheet webs of

Many experiments were made with the larvae of A. fuscus and A. museorum in order to determine to what extent, if any, they were immune from the attacks of Tegenaria domestica, about the webs of which they were most frequently found. The larvae were also associated with other household spiders which were not identified, and they were common under the tiles of an outhouse near the webs of Clubionia terrestris. The larvae of these two species of Anthrenus are structurally nearly identical, and A. fuscus and/or A. museorum were used in the experiments described below, so that the following remarks apply to both species. Anthrenus larvae are very similar in their essential features to those of Ctesias serra. They are clothed with long and stiff bristles, have tufts of sub-recumbent, multi-segmented, spear-headed hairs which can be suddenly erected and expanded in varying degrees on the postero-lateral part of the fourth to seventh abdominal tergites, and have a

caudal brush consisting of a few long and slender hairs which can be rapidly vibrated. They are capable of erecting and expanding the dorsal tufts more or less independently of each other, but usually all four tufts of the side which is stimulated will be more rapidly and completely erected and expanded than those of the opposite side. The erection of these tufts is usually accompanied by a downward tilting of the side of the body attacked, presumably in order to protect the ventral surface and simultaneously bring the tufts of

the other side nearer to the point of attack.

Many larvae (about 50) were dropped in the webs of many different individuals of T. domestica. The impact on hitting the web frequently drew the attention of the spider to the larva, in which case it was immediately attacked and eaten. This was particularly noticeable where half-grown spiders were concerned. When the larva was gently and carefully placed in the web, or when for some other reason it was not immediately noticed, it usually managed to escape. Larvae put in the webs sometimes began to crawl almost immediately, but they frequently remained for considerable periods, often for 1-3 hours, where they were placed. One larva placed in a web at 6 p.m. (18.vii.42) was still in the same position 24 hours later! As it appeared to be dead it was picked up and, when found to be still alive, immediately replaced. When this larva was examined about two hours later it was found to be crawling on the lower surface of the web. A number of the larvae placed in webs bored through the web and effected their escape by crawling on the lower surface. Larvae placed in webs of full-grown or nearly fullgrown Tegenaria were not attacked so frequently.

A Tegenaria about 8 mm. long was kept without other food for a month in a petri dish with four mature larvae, and during this time two larvae escaped and the remaining two showed no signs of having been attacked and were still alive when the spider died. Two mature larvae were confined in a bottle with four Salticids (two species), and at the end of two weeks the

spiders were dead and the larvae were feeding on them.

Under natural conditions apparently few larvae are successfully attacked. No "chewed" larvae have been found in the insect remains accumulated below the webs of Tegenaria. Apart from the fact that they are to some extent protected by their long and stiff setae and their ability to bring into play two kinds of warning movements when alarmed, they are not attacked for two important reasons. Firstly, the larvae live most of the time near but not available to the spiders, among the dead insects below the webs or in those that are left in disused webs. The larvae are also often inside the dead insects, so that in any case it would be impossible for the spiders to get at them. Secondly, when they do happen to crawl on the web itself they do so very slowly and apparently without attracting the spiders, as they are able to crawl here without becoming entangled. Furthermore, the only larvae that have been found on webs were found crawling on the lower surface. experiments mentioned above, inconclusive as they obviously are, suggest that a larva finding itself in a web has a tendency to bore through and crawl on the lower surface where it would naturally be more immune from attack by the spider.

Anthrenus museorum L.

This beetle is nearly cosmopolitan in distribution and is one of the best-known beetles attacking dried insects and other museum specimens. It has often been recorded damaging skins, furs, feathers, horns, woollens, and silk.

Abderhalden (1925) claims that larvae develop normally and produce adults when fed on threads of pure natural silk (silkworm) and that they would also live on spider silk (Avicularidae). I have kept two larvae with silk from the egg sac of Tegenaria domestica for more than three months (27.vii.-3.xi.42), and during this period they have moulted a few times and decreased in size but a microscopic examination of the silk shows that they have not even begun to gnaw the strands. On several occasions I have given larvae kept in captivity egg sacs containing dead eggs or young spiders, and in all these instances the larvae bored through the egg sacs in order to feed on the contents. Similarly, about sheds and barns I have found them in spider egg sacs and in moth cocoons through the silk of which they had bored. However, I have

never seen them attacking uninjured egg sacs.

The adults are found in the spring and early summer on various flowers, particularly Umbelliferae, where they feed on pollen and nectar. Those collected in June and July in Linton appeared to prefer parsley, though they were also found on various other flowers, e.g. daisy, privet, and cow parsley. In Linton the number of adult beetles dropped off rapidly in the second week of July, whereas the adults of A. fuscus were still plentiful in the first week of August. The following brief summary of the life-history is compiled from the contributions of various writers. After copulation the female usually becomes negatively phototropic and enters houses, etc. in order to find a suitable place in which to oviposit. The pre-oviposition period is 3-7 days, and 21-35 eggs are laid. The larvae usually take 7-14 months to develop, and there is, as a rule, only one generation a year. At 18° C. the larvae take 10–11 months to complete their development. The number of moults is variable, but usually appears to be about ten. Out of doors the winter is passed in the larval stage. Pupation usually occurs from April to July, and the pupa remains within the last larval skin. At 20°-22° C, the pupal stage takes 9-10 days, the adult remains within the last larval skin for 4-5 days, and the active life of adult males is 10-14 days and that of adult females 12-18 days.

The means by which the larva is protected from the attacks of spiders has already been discussed above when dealing with A. fuscus. The only previous record of its occurrence in cobwebs appears to be that of Rüschkamp

(1921).

Trinodes hirtus F.

This European species has been recorded many times in and about spider webs in Britain and on the Continent. It is found in spider webs under bark, in hollow trees, and among ivy and also in houses, barns, and old buildings (Chapuis and Candéze, 1855; Douglas, 1859; Fowler, 1889; Ganglbauer, 1904; Everts, 1905; Wradatsch, 1917; Wanka, 1918; Dollman, 1913; Rüschkamp, 1921; Donisthorpe, 1930). Unfortunately the spiders in the webs of which it has been found have seldom been identified. Ganglbauer (1904) and Everts (1905) record the fact that the larvae are sometimes found feeding on insects entangled in the webs of the common house spider, Tegenaria domestica L. Although most of the published notes on the habits of the larvae refer to their occurrence in and about spider webs, they are able to maintain themselves on the remains of caterpillars and other insects which are sometimes numerous under bark and which have not been killed by spiders. In captivity the larvae have been reared on dead flies (Donisthorpe, 1930). The winter is passed in the larval stage, and pupation occurs in May and June. The pupae always remain

within the last larval skin, and they may sometimes be attached to the

underside of the spider web (Chapuis and Candéze, 1855).

According to Ganglbauer (1904), the larvae of T. hirtus can run very quickly over the web of Tegenaria. In this species, unlike all other known forms associated with spiders, there are no erectable dorsal tufts of spearheaded hairs nor is there a caudal brush. However, there are numerous dorsal and lateral bristles which are relatively much stouter and longer than in the other species found with spiders, and these probably give Trinodes an immunity from attack which is only achieved in other species by erecting the dorsal tufts and, or, vibrating the caudal brush. T. hirtus often partly curls up when alarmed, and in this way no doubt succeeds in protecting its vulnerable ventral surface.

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³ This bibliography includes only those papers in which some mention is made of DERMESTIDAE in cobwebs or Dermestids feeding on spider's silk.

OBSERVATIONS ON THE NYMPH AND ADULT OF EPHEMERELLA NOTATA EATON (EPHEMEROPTERA)

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In early May, 1942, we paid a brief visit to the R. Eden to obtain specimens of a Caddisfly, the Grannom (Brachycentrus subnubilus Curt.) and at Eden Bridge, near Temple Sowerby, amongst other insects we collected a number of nymphs of Ephemerella. These nymphs were found among strands of Fontinalis (Water Moss) on stones, and on examination were seen to differ in several characters from nymphs of E. ignita (Poda). The R. Eden is the type locality for E. notata Etn., and it seemed not unlikely that these nymphs might belong to that species. An examination of Ephemerella nymphs from Kildare, on the lower reaches of the R. Liffey (where E. notata also occurs), revealed two types of nymphs, one the typical E. ignita and the other identical with those from the R. Eden. The identity of these R. Liffey nymphs with E. notata had been established beyond doubt by the discovery of hatching nymphs in the stomachs of brown trout taken at a time when only E. notata duns were emerging and when no E. ignita were on the wing.

The imagines and subimagines of *E. notata* have been described by Eaton in his Monograph (1883–88) and since that time there have been few references to the species in entomological literature. This paucity of records may possibly be due to the superficial resemblance of *E. notata* to *Heptagenia sulphurea*, causing it to be overlooked by both anglers and entomologists, but it is probable that this insect is restricted to a narrower range of environmental conditions (stenoecic) than is *E. ignita* and consequently more localised in its geographical

distribution.

Eaton's specimens were taken at Langwathby and Salkeld, on the R. Eden, and he also records a single subimago in Mr. King's collection from the "south of Scotland." On the Continent it has been recorded from Germany, Thüringer Wald and München (Ulmer 1929), Lohr, Gemünden and Langenprozelten am Main (Schoenemund 1930) and from Belgium (Ulmer 1929). The distribution of the species in the British Isles, as at present known, is as follows:—Devon: Bovey Tracey, 3.vi.1931. Surrey: R. Wey, between Tilford and Elstead, 28.v.1933. Radnor: R. Ithon, Llandrindod Wells, August 1912. Yorks: R. Nidd, Ripley, 16.vi.1925; R. Wharfe, above Grassington, 23.vi.1926; R. Wharfe, Boston Spa, 27.v.1927 (nymphs). Cumberland: R. Eden, Langwathby and Salkeld, 13-27.vi.1885; R. Eden, Eden Bridge, 8.vi.1942 (nymphs); R. Eden, Briggle Beck, Skirwith, 19.vi.1924. Derry: Moneymore, 5.vi.1933. Cavan: R. Annalee, Cootehill, 2-12.vi.1936. Meath: R. Boyne, near Trim, 22.v.1935. Kildare: R. Liffey, Clane, Proc. R. Ent. Soc. Lond. (A) 18. Pts. 4-6. (June 1943.)

12.v.-1.vi.1935; Straffan, 7.vi.1930, 22.v.-10.vi.1935, 22.v.1936, 23.v.-

12.vi.1937, 8.v.1938.

We have seen examples from all the above British localities except the R. Ithon. In spite of the fact that these specimens were identified by Eaton himself (South 1913), the unusually late date for that record raises an element of doubt and the occurrence of the species at Llandrindod Wells requires confirmation. The Irish records (except that from Derry) are based on collections and observations made by the late Mr. R. Southern and one of us (W.E.F.) from 1930–38. The specimens taken at Straffan on 7th June, 1930, were

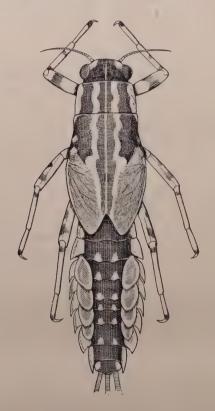


Fig. 1.—Ephemerella notata Etn., nymph imes 10.

identified by Mr. Southern, who recognised that the capture constituted an addition to the list of Irish Ephemeroptera. In the course of work and angling excursions, many reaches of the Liffey were visited but *E. notata* was found only in those places where the river flowed over limestone rocks and the water was alkaline in character, such as at Straffan. Considering the foregoing list of localities, it is interesting to note that all the streams appear to be situated either on lime-bearing rocks or else to receive their water as drainage from such rock-formations. The Eden, for example, at Eden Bridge, Skirwith, and Salkeld flows over New Red Sandstone, but most of its water drains from the surrounding Carboniferous Limestone. Tilford and Elstead, on the R. Wey, are situated in an area of Lower Greensand, but much of the water is

received from the Chalk Downs to the north and west. Other factors which may affect the distribution of this species are the size and rate of flow of the river, factors which are themselves influenced by the configuration of the land and the amount of rainfall. Small becks and streams do not appear to be suitable for notata, although they will support E. ignita. The presence of Fontinalis is not necessarily a factor, since on the Liftey this plant occurs at both Ballysmuttan (where the river flows over granite and is acid in character) and Straffan, but E. notata is absent from the former station.

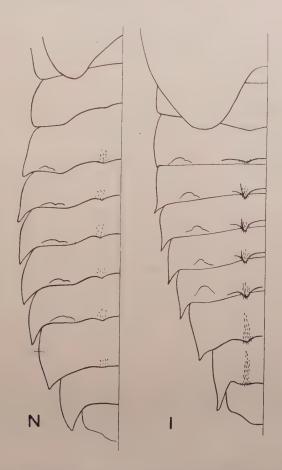


Fig. 2.—Dorsal abdominal armature of N, E. notata, I, E. ignita nymphs. Left half only of each abdomen shown, gills omitted.

Schoenemund (1930) was the first to recognise the nymph of *notata*. He separated it from *ignita* as follows:—

Underside of abdomen brown to blackish ("dunkelfarbig"), on each side with a fine, somewhat oblique, very conspicuous black line

Ephemerella ignita (Poda).

The Eden Bridge examples showed considerable variation in the depth of colouring of the underside of the abdomen, some of them having a median longitudinal dark brown stripe, as dark as in *ignita*; his second character, the "fine, somewhat oblique, very conspicuous black line" on each side of the

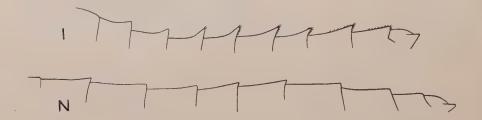


Fig. 3.—Profile of abdominal tergites, N, E. notata, and I, E. ignita.

sternite is often more noticeable in *notata* than in *ignita*, in which it is frequently concealed by the brown ground-colour. Admittedly *E. notata* shows, in addition, the characteristic two pairs of ventral spots on the abdomen from which

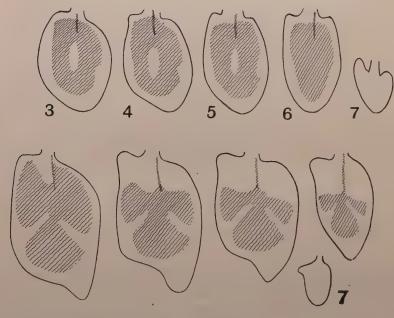


Fig. 4.—Gill lamellae of abdominal segments 3–7. Upper row, $E.\ notata$, lower row $E.\ ignita$.

the adult takes its name, but these are sometimes obscured by the dark median band.

Comparison of the nymphs of notata and ignita has revealed several other differences, some of them structural, which appear to offer more useful dis-

tinctions than those given by Schoenemund. Firstly there are the caudal setae or "tails"; in *ignita* these are marked with alternate broad brown and whitish bands, and the apices of the segments are set with whorls of short spines, whereas in *notata* the tails are whitish throughout, being at most only finely ringed with brownish at the joints. The apices of the segments carry whorls of short spines only towards the base of the setae, the remaining part being fringed with hairs. The dorsal tubercles on the abdominal segments in *ignita* are strongly produced, and in side view noticeably elevated; in *notata* they are much less strongly produced and but slightly elevated (figs. 2, 3). Schoenemund uses as a generic character for *Ephemerella* the possession of strongly projecting tubercles on the hind margins of the tergites. Such are certainly not present in nymphs of *E. notata* which I have examined.

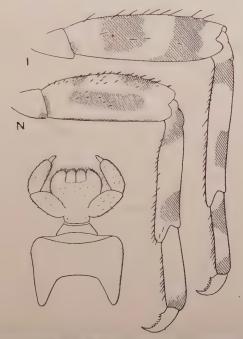


Fig. 5.—Median legs of nymphs of I, E. ignita, and N, E. notata, and labium of E. notata.

The gill lamellae of abdominal segments three to six are different both in outline and in the shape of the pigmented pattern in the two species (fig. 4). In *ignita* the inner apical angle is very definitely produced, and the pigmented area is shaped somewhat like a clover-leaf. In *notata* the apical angle is rounded, and the pigmented area roughly duplicates the shape of the lamella, with a pale ovate spot in the centre of the first three lamellae. The gill-cover of segment seven (fifth gill) in *notata* has two basally directed lobes at the base which are absent in *ignita*.

The setae on the dorsal carina of the femur in *ignita* are sparse and moderately long, whereas in *notata* they are much denser and short (fig. 5). The tarsus in *ignita* is dark with a pale band before the apex; in *notata* it is pale with a dark apex. There are also slight differences in the mouth-parts, particularly in the proportions of the palpal segments. The maxillary palpi in *notata* beginning with the basal segment are 43:24:20 and in *ignita* 21:12:30.

The labial palpi in notata (fig. 5) are stouter, the terminal segment being re-

latively shorter and narrower than in ignita.

Nymphs of both species are subject to variation in colour and pattern; *E. ignita* particularly so. *E. notata* has often a pair of pale dorsal stripes on the thorax which are continued as pairs of spots on the abdominal tergites (fig. 1). Ventrally the lateral flanges of the abdominal segments are usually pale in *notata*, although the middle portion of the segment may be darker.

In some respects, especially in the fringed nature of the caudal setae, the less produced dorsal tubercles and the form of the fifth gill lamella, E. notata nymphs recall those of the genus Chitonophora, and examples of notata might conceivably run out to that genus in Schoenemund's key (1930). The shape of the fifth gill as figured by Lestage (1917), however, differs from that figured by Schoenemund. The former shows the basal lobes projecting outward (Chitonophora sp.), the latter with them directed basally (Chitonophora krieghoff). The proportions of the palpal segments also approach those of Chitonophora. The imaginal characters of E. notata, however, appear to us clearly to be those of Ephemerella. In the absence of authentic material of Chitonophora, it is not proposed to consider here the claims of this genus to generic rank. There is something to be said for the view put forward by Traver that it should be treated provisionally either as a group or subgenus of Ephemerella.

It has already been mentioned that little is known about E. notata and therefore the following account of its habits may interest the entomologist and also the fly-fisher. Its emergence period on the R. Liffey extends from 10th May to 12th June, and records from other waters prolong this period to 27th June. The transformation from the nymph takes place soon after sunset, the duns appearing in large numbers on the water. The bright yellow body and whitish-grey wings tinged with yellow which characterise both sexes makes the dun of E. notata a most conspicuous "fly" even at dusk. At first glance, as has already been suggested, it might be confused with Heptagenia sulphurea (known to anglers as the "Little Yellow May Dun" or "Yellow Hawk"), but the latter has only two tails (setae), and its colouring is less intense, being, as its name suggests, more sulphur-yellow. H. sulphurea may also be seen on the water during May and June, and the fact that on the Liffey the two species sometimes share the name of Yellow Hawk is evidence that such confusion does exist.

There are few observations on the spinners, but those we have, suggest that the flies are on the wing in the afternoon and early evening in fine hot weather. From two observations made on the R. Wey (Kimmins 1933) it seems likely that the nuptial flight of the spinners may take place at some distance, i.e., 200 yards from the water. The female spinners carry their egg-masses in a manner similar to that of E. ignita, but we have no information whether or no

they fly upstream before oviposition, as in that species.

Angling experience on the R. Liffey, and the examination of stomach contents of brown trout taken from that river during the hatch, show that the fish feed predominantly on the emerging nymphs, although some duns are also eaten. When the fish are feeding thus at dusk it has been found that the artificial flies "Yellow Sally" (a representation of the stonefly *Isoperla*) and "Yellow May" fished dry may be usefully tried as imitations of the duns, since both may be dressed with yellow wings and hackle. A sunken "Yellow Sally" was taken well by the fish, presumably because it resembled the emerging nymphs on which the fish were chiefly feeding.

It is curious that this fly, which is so distinctive, does not appear to be

mentioned in angling literature. Further information about its geographical distribution is desirable, but it would seem to be far more localised in its occurrence than is the closely related and well-known *E. ignita* (Blue Winged Olive), a fact which may partly account for this neglect. The late hour at which the duns emerge, the comparatively short period of the season during which the flies are on the wing, and the superficial resemblance to *H. sulphurea*, may also have contributed to its having escaped the notice of anglers.

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THE FUNCTION AND COMPARATIVE ANATOMY OF THE OREILLETS IN THE ODONATA

By Lt.-Col. F. C. Fraser, I.M.S. Retd., F.R.E.S.

THE "oreillets" or "auricles" which are found in a number of families belonging to the Order Odonata and more especially in those belonging to the suborder Anisoptera, are two small processes or outgrowths placed one on each side of the second abdominal segment of the male imago, and are so-called on account of a fancied resemblance to the human ear. They occur also as complementary but extremely rudimentary and functionless organs in the female

(figs. 1, 0, 12 and 13).

The comparison of the shape of the oreillets to that of the human ear is useful for descriptive purposes but it should be understood that the organ, as it exists in the Odonata, resembles an inverted human ear and that the helical border of this ear is furnished with spines or denticles. The narrowest part of the oreillets corresponding to the lobe of the ear is not sharply defined but is bevelled off obliquely on to the side of the abdomen. The organs are broadly sessile, their base lying somewhat obliquely as viewed from below, and they project at a variable angle from the sides of the abdomen, so that a more or less deep and narrow notch or recess, facing rearwards, is formed between the helical border of the oreillet and the abdominal wall. The helical spines number from two to fifteen according to what species they are found in, but they may be replaced by tiny denticles, in which case their number and the space which they occupy is greatly increased; they may indeed be spread over most of the outer surface of the oreillet, arranged in moderately regular oblique rows (figs. 2, 3, 4, 12 and 13).

Except for the genera *Hemicordulia*, *Hemianax*, *Anax* and *Anotogaster* and the whole of the Libellulidae, or eillets are present throughout the suborder Anisoptera. They are absent in the suborder Anisozygoptera as represented by the sole living species *Epiophlebia superstes* (Selys) and a number of fossil species, which latter, however, are too poorly preserved to show these structures even if present. They are generally absent throughout the suborder Zygoptera, but in some genera belonging to the family Epallagidae are quite well developed. From their sporadic occurrence in this last suborder, it is possible that they may have originated independently of those of the suborder Anisoptera, and that although analogous they are not homologous.

In the course of this investigation, it has been found that the oreillets are similar in all species of any particular genus, so that they possess a hitherto

unsuspected generic value.

In those genera where the oreillets are rudimentary or absent, viz. Hemicordulia, Hemianax, Anax and Anotogaster, and in all genera belonging to the family Libellulidae, the hind-wings are rounded at the tornus instead of being strongly angulated and more or less deeply excised as in the others. This is obviously more than a coincidence, and most certainly proves that the two conditions are correlated. Two possible explanations suggest themselves, viz. either the oreillets serve to fill in the gap of the hind-wing, or the wing is excised in order not to impinge on the oreillets during flight. The former explanation has so far held the field. Tillyard (1917), in his Biology of Dragonflies (page 32), referring to the oreillets, has given his opinion as follows:—"Their function is

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unknown; but it seems fairly clear, from the method of occurrence, that they must act in conjunction with the anal angle of the wing in controlling flight. Otherwise it would be difficult to account for their absence in Anax, Hemianax and Hemicordulia, the only genera of the Aeschninae and Cordulinae which

have rounded wings in the males."

To me, such an explanation seems utterly illogical, for I find it hard to believe that evolution, which is dependent on selection of what is best for the organism, should first create a defective wing and then proceed to patch it up by the clumsy expedient of producing an excrescence from the side of the abdomen to fill in the gap. The dragonfly wing, throughout the ages, has shown itself to be of so plastic a nature that any defect would necessarily be corrected by some change in its shape or venation. Thus I believe that the oreillets perform some other function which has not been so far discovered, and I am compelled to fall back upon the alternative explanation which I have mentioned above, that is, that the wings are excised secondarily in order to clear the oreillets during flight.

In coming to this conclusion, I have asked myself the following questions,

to which subsequent investigation has given the appended answers:

(1) Do the oreillets adequately fill the gap in the base of the hind-wing?

After examining a large number of different species, it can be said with certainty that they do not; moreover the discrepancy between the size of the oreillet and the excision in the wing is so wide that one wonders how such a theory came to be put forward. Even in the species Gynacantha membranalis (Karsch), where the size of the oreillets is enormous, they do not nearly fill the gap in the hind-wing. In some species, I find that the oreillets do not entirely correspond with the site of the gap in the wing (fig. 1).

(2) Can the oreillets possibly assist in controlling flight as Tillyard has

suggested?

This is more than doubtful since they are immobile organs and could only act occasionally and momentarily in conjunction with the wings when the two happened to coincide or lie in the same plane.

(3) If the function of the oreillets is merely to fill in a defect of the wing, for what purpose are they furnished with a row of spines along the posterior

border ? (figs. 3, 4 and 12).

It is self-evident that such an armature can have no relation whatever to flight. From the position of the spines and the fact that they are turned inwards, it would seem also that they serve no protective function. The function of the oreillets ought to explain the presence of the spines.

(4) Do the oreillets occur in any species in which the hind-wing is neither

angulated nor excised at the base?

Yes; they occur in several species of the Gomphidae where the base of the hind-wing is greatly reduced and strongly splayed outwards so as to arch widely away from the neighbourhood of the oreillets (fig. 7). In the genus Indophaea, where oreillets occur, the base of the wing is practically petiolated and so lies remote from these organs (figs. 5 and 6).

(5) Why are the oreillets absent in those species with rounded hind-wings?

Has some other organ taken over their function?

The answer to the second of these questions serves to answer the first, for I find that there are certain devices which appear to serve the same purpose as do the oreillets.

(6) Are the oreillets correlated with any other important structures besides

the hind-wings?

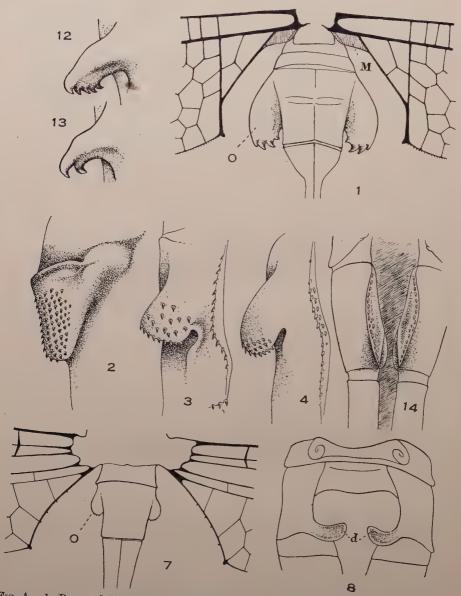


Fig. A.—1. Bases of hind-wings and abdomen of Gynacantha membranalis Karsch; O, oreillets, M, membrane. 2. Oreillet of Petalura gigantea Leach. 3. Oreillet of Tachopteryx pryeri Selys. 4. Oreillet of Cordulegaster annulatus Latr. 14. Ventral aspect of the 2nd abdominal segment of Anax parthenope Selys (details of genital sac omitted). 7. Bases of hind-wings and abdomen of Echinopterogomphus africanus Fraser; O, oreillets. Note the discrepancy in the size of the latter and the notch in the hind-wing. 8. Ventral aspect of Lyriothemis magnificata (Selys), a typical Libelluline (details of genital sac omitted). d. Genital lobes, which probably function as oreillets.

Yes; they lie close to and one on each side of the male genitalia which, if it be not a coincidence, is at least significant. A consideration of this relationship suggests two possibilities: the oreillets may act as accessory hamules in the act of copulation or they may act as "locators" or "directors" to the female preceding that act (fig. 5).

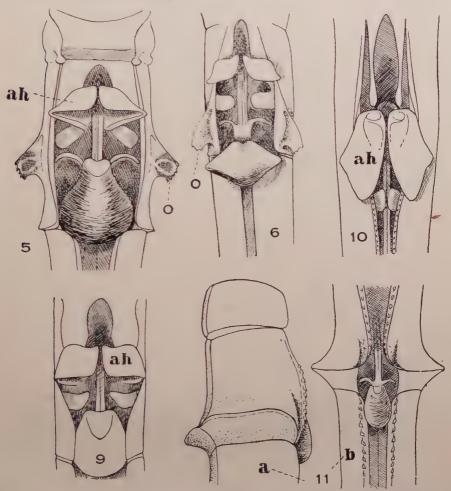


Fig. B.—5. Genitalia of Indophaea cardinalis Fraser, with,—O, oreillet on either side of genital sac. ah, Anterior hamules. 6. The same of Euphaea subnodalis Selys. 10. Genitalia of Perilestes attenuata Selys. Note the divaricate anterior hamules, ah, which probably act as oreillets and are typical of the whole Legion Lestes. 9. Typical genitalia of a Coenagrionine. ah, Anterior hamules. 11. a, 1st, 2nd and base of 3rd abdominal segment of Rhinocypha cucullata Selys, dorso-lateral aspect, showing the apical ruff-like expansion on the 2nd segment, which acts as an oreillet. b, The same, ventral aspect (details of genital sac omitted).

Lying, as they do, outside the genital sac, and rigid by nature, it is difficult to see how the first of these functions could be performed, so that I consider that this possibility must be dismissed as impracticable. The second function is, however, open to experimental proof, for a glance at the position of the

oreillets will show that anything approaching the genital sac from behind or laterally will be certain to meet with obstruction from them. This will be better appreciated if the tip of the finger be run lightly alongside the abdomen towards its base, when it will be infallibly arrested by the imbricated spines lining the helical border of the oreillet. If the finger-nail be employed instead, it will be found that it slips into the notch between the oreillet and abdominal wall. So effectual is this obstacle, that if force be employed, the abdomen will buckle up. If now, to complete the experiment, a female abdomen be substituted for the finger, the same result will be obtained. If the ovipositor of any female be examined, it will be noticed that the valves covering the terebra are prolonged apically so that a deep notch is formed between the apex and the abdominal wall; it is this notch which interlocks with the notch on

the lower border of the oreillet (fig. 6).

When it is considered that the act of copulation is performed blindly by the female and often during flight when she is slung by her head from the male anal appendages, swinging from side to side pendulum-wise, it will be appreciated that some such guide as I have mentioned would much facilitate the act and assist her in her blind groping for the male genitalia. As she brings her abdomen forward she comes into contact with that of the male, and following it along towards the base, is soon brought up abruptly by the interlocking of her vulvar scales with the oreillet. No matter on which side of the male abdomen she makes her approach, she is certain to contact one or other of these organs unless she is fortunate enough to make a lucky shot the first time. Should she foul the oreillet, all she has to do is to disengage herself, move her abdomen a slight distance medially and contact is at once made between the two sets of genitalia. The whole act, accomplished as I have described, seems so entirely natural that I am satisfied that the true function of the oreillets is to act as "directors" for the female during the act of copulation.

One further question remains, which seems to me to be the most difficult

for which to find a satisfactory answer:

"Is the correlation between the shape of the base of the hind-wing and

oreillets more apparent than real?"

Undoubtedly the deep excision in the hind-wing has been evolved in order to clear the oreillet during flight, otherwise, even though the discrepancy between the size of the notch and that of the oreillet is often large, it is conceivable that a rapidly whirring wing might need the extra space in order not to foul the oreillet on occasions. But I believe that the produced tornus and notch act as additional directors to the female during the act of copulation. The hind-wing of a dragonfly is employed more as a supporting plane than as a driving force: hence the greater expanse over that of the fore-wing, and so it would be possible for the female to come into contact with the basal border of the wing when groping rather widely for the male genitalia. Figs. 1 and 7 show clearly how the wings are held wide like a pair of outstretched arms to intercept anything approaching from behind. They may act in very much the same way as do the oreillets, only on a magnified scale. The extensive "membrane" lining the basal border of the hind-wing may play some part in this function, and serve to orient the female in her attempts at copulation. No function has so far been attributed to this membrane (fig. 1, m).

The rounding off of the base of the hind-wing (in the absence of the oreillets) may be only an associated item in the higher scale of evolution reached by species possessing these characters. For I find that all those species with a rounded base to the hind-wing are of recent origin as opposed to the more

archaic ones with angulated and excised wings. Thus in the super-family Libelluloidea, the Libellulidae, with a rounded base to the hind-wings, are of recent origin, whilst the Cordulidae, with angulated and excised base, are much more primitive; in the latter family, the genus *Hemicordulia* is quite the most recent and is the only one in the family which possesses rounded bases to the hind-wings. A parallel case is found in the genus *Hemianax* of the family Aeshnidae. Thus it seems to me that the rounded hind-wing and the absent oreillet are not so much correlated as symptomatic of that perfection and simplification which is associated with a higher scale of evolution.

Only a brief and incomplete summary can be given here of those devices which perform the same functions as do the oreillets in species which do not possess the latter organs. It has been generally supposed that the possession of oreillets is confined to certain families and genera of the suborder Anisoptera (Gomphidae, Cordulegasteridae, Aeshnidae and Cordu-LIIDAE), although actually they are also present in the large family EPALLAGIDAE of the Zygoptera. But whereas in the Anisoptera one finds the oreillets confined to the more primitive families and genera, in the EPALLAGIDAE it is just those primitive forms which are without these organs! They are quite absent in the genera Epallage and Dysphaea; of rather primitive build in genus Allophaea, a slightly more recent one than the preceding, and then progressively more highly developed as one passes to the more highly specialised genera such as Indophaea and Euphaea. This extraordinary reversal of the conditions found in the Anisoptera I consider must be due to an entirely independent development of the oreillets in the EPALLAGIDAE, although they are similarly situated and doubtless perform the same function. In all these genera of the EPAL-LAGIDAE, the wings are almost petiolated at the base, so that no possibility of correlation with the wings and flight arises. In the primitive genera Epallage and Dysphaea, the function of the oreillets appears to be performed by a row of stout spines which border the genital sac on each side, arising from the edges of the urotergites; these spines are absent in those genera which possess oreillets (figs. 5 and 6).

Apart from the EPALLAGIDAE, the rest of the Zygoptera appear to depend on other devices, the principal one of which I believe is the pair of projecting and widely splayed anterior hamules of the male genitalia: these two organs together form a deep funnel-shaped recess situated immediately in rear of the genital sac so that the female genitalia approaching from behind would slip into it and come to rest at the very door of the genital sac. Throughout the Zygoptera, except for the Lestidae where the anterior hamules form an important family character, these organs are wider than broad, their inner borders are closely apposed and their posterior borders are in a straight line horizontally transverse to the longitudinal axis of the abdomen. In the Lestidae the posterior part of the hamules is prolonged distally so that the inner borders are strongly divaricate and splayed outwards: thus the female genitalia coming into contact with this border would be guided obliquely medially to the

genital sac (figs. 9 and 10).

An examination of the genitalia throughout the Zygoptera will probably reveal some curious devices, but here two only can be mentioned. In Anisopleura, the ventral surface of the second abdominal segment presents a transverse and very prominent ridge, somewhat cupped posteriorly. This ridge stands immediately posterior to the genital sac and, in a pair of A. comes, still in cop., which I possess, the apices of the vulvar scales are seen to be nestling in the pocket formed by this ridge. Again in Rhinocypha cucullata (Selys)

the joint between the second and third abdominal segments of the male is expanded into a prominent node, which forms a collar or ruff surrounding the abdomen. This dilatation is formed by the apical border of the urotergite of the second segment which is curled strongly outwards and, viewed laterally, looks in silhouette just like the oreillets of *Indophaea*: I have no doubt in my own mind that it performs a similar function, for it stands at the entrance to the genital sac and no other conceivable use for it can be assigned (figs. 11a

and b).

In the Anisoptera great variability in the size and shape of the oreillets is found, ranging from a mere ridge or tubercle coated with fine denticles. the Gomphidae the posterior border of the oreillet may bear some imbricated spines and the adjacent area be coated with denticles (as in Onychogomphus), or only the spines are present (as in Lamelligomphus), or the denticles alone (Gomphus, Macrogomphus etc.). In the Aeshnidae the oreillets are usually of the conventional ear-shape and the posterior border is furnished with from 2 to 5 spines: in Anaciaeshna there are, in all species, only 2 spines (figs. 12 and 13). Throughout the LIBELLULIDAE the oreillets are absent but there is an oblique carina minutely spined in the same situation. I think that, in them, the function of director is taken over by the genital lobe, or the prolongation or expansion of the apical end of the urotergite ventrally. No function has been assigned hitherto to this organ, yet, from its innumerable shapes and from the way it projects over the apical entrance to the genital sac, it must be of some great importance to the insect and could act admirably as a substitute for the oreillets. During copulation, I conjecture that the urotergites would separate widely so as to distend the opening of the genital sac, in which case the genital lobes would become more or less widely divaricate and be in a position to arrest the female genitalia as it felt its way forward (fig. 8, d).

In Hemianax, where the oreillets are absent, the borders of the urotergite are expanded and form a flattened elongated triangular plate robustly spined along its outer border and ending in a spine apically (fig. 14). It is quite probable that this plate acts as a director to the female. In this genus also the "membrane" of the wing is of comparatively enormous expanse and tends to overlap the base of the abdomen. What function this membrane can perform is a mystery: it is present in fore- and hind-wings alike, although purely vestigial in the former, and it is present in both sexes and about uniformly developed in the two. It is opaque in character, unlike the rest of the membrane of the wings, and its free border is unsupported by any strong vein; it can neither strengthen the wing nor assist in flight owing to its flimsy character; thus it may be sensory in nature and enter into the function of copulation. In those species with deeply excised wings and large or eillets, the membrane is largely obsolescent (fig. 1). One is tempted to think that the absence of or eillets in the most recent forms of the Anisoptera is due to their more highly educated

sense and so to their ability to dispense with guides.

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Smith, A., 1936, New species of Coccidae, Proc. R. ent. Soc. Lond. (B) 6:301-306, pl. 1.

. 1936, New species of Coccidae, Trans. R. ent. Soc. Lond. 84: 901-936.

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